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Abstract

Terminal Ediacaran metazoan reefs (~548-541 Million years ago (Ma)) can be locally substantial and the skeletal metazoans *Cloudina riemkeae, C. hartmannae, Namacalathus* and *Namapoikia* produced diverse reef types with complex ecologies in association with varied microbialite support or influence. In the Nama Group, Namibia, metazoan reefs grew in three associations with differing dominant frameworks: 1) Monospecific aggregations of *Cloudina*, 2) *Cloudina – Namacalathus –* thrombolite assemblages, and 3) Thrombolite-dominated metazoan communities. *C. hartmannae* formed monospecific reefs up to 7 m wide and 3 m high with no microbialite component. Synoptic relief was probably less than 1 m. *C. riemkeae* formed densely-aggregating assemblages associated with microbialite and thrombolite, each from 30 to 100 mm high, which successively colonised former generations. Isolated *Namacalathus* either intergrew with *C. riemkeae*, or formed dense, low-relief, monospecific aggregations succeeding *C. riemkeae* frameworks. Thrombolite-dominated metazoan reefs could reach up to 20 m in height and width, with synoptic relief of up to several meters. *Cloudina* and *Namacalathus* grew closely associated with these framework thrombolites, and *Namapoiki*a, which was encrusting and modular, reached up to 1m in size and occupied neptunian dykes and fissures. *Cloudina* and *Namacalathus* also grow

cryptically, either as pendent aggregations from laminar crypt ceilings in microbial framework reefs, or as clusters associated with thrombolite attached to neptunian dyke walls.

Keywords: Reefs, Ediacaran, Cambrian, Competition, Palaeoecology

While metazoans may have had an origin around ~800-750 Ma, they did not reach ecological dominance as manifest in the geological record until the Ediacaran-Cambrian transition (Erwin et al., 2011). The first appearance of metazoan fossilizable hard parts in the latest Ediacaran (~550 Ma) and the subsequent radiation of skeletons over the succeeding 25 million years of the Cambrian (Knoll, 2003) marks a profound transition in Earth's history. But by the end of the Proterozoic, diverse mineralized skeletons are thought to have evolved in protists, plants and animals, using calcite, aragonite, phosphate, as well as silica. Calcareous biomineralization changed carbonate sediment production from one of solely inorganic and microbially-mediated precipitation driven by evaporation to a system under considerable biological control. Today, nearly all calcium carbonate leaves the oceans as skeletons, which form in a wide range of both shallow marine and open oceanic settings, but particularly within reefs. The evolution of the reef-building habit is a significant ecological innovation, involving close aggregating growth, permanent fixture to a hard substrate, and the creation of topographic relief with internal complexity on the seafloor. Reefs are an important focus of biodiversity in modern ecosystems, and have been since their inception (Wood, 1999; Penny et al., 2014). As such, the rise of marine metazoans, the onset of biomineralization, and the inception of metazoan reefs marks a step-change in the workings of the global carbon cycle.

The acquisition of calcareous and phosphatic skeletons reflects multiple, independent co-optations of molecular and physiological processes that are widely

shared among eukaryotic organisms (Westbroek & Marin, 1998): indeed the biochemical supply of ions and the assembly of the necessary genetic and biochemical machinery for biomineralisation may be an ancient feature of eukaryotes (Aizawa & Miyachi 1986). The chemical reaction [$CO_2 + H_2O \leftrightarrows HCO_3^- + H^+$] underlies many fundamental physiological processes including processing of metabolic wastes, regulation of pH, carbon fixation, and ion transport across organic membranes (Henry, 1996). Any enzymes that catalyze this process, such as metalloenzyme carbonic anhydrase, will also aid skeletal formation as HCO_3^- in turn reacts with Ca^{2+} to produce $CaCO_3$.

Metazoan hard-parts in the Ediacaran are represented by non-mineralised and mineralized tubes (Hahn et al., 1982; Grant, 1990; Ivantsov, 1990), possible, but as yet unverified, siliceous sponge spicules (Reitner & Worheide, 2002), and supportive calcareous skeletons, including *Cloudina* (Germs, 1972; Grant, 1990), *Namacalathus* (Grotzinger et al., 2000), and *Namapoikia* (Wood et al., 2002). These calcified taxa are of uncertain affinity, but may represent stem group Eumetazoa, Cnidaria and Bilateria (Wood, 2011; Zhuravlev et al., 2015). All were sessile benthos and grew in equatorial, shallow marine carbonate settings, and probably become extinct at the end of the Ediacaran (Amthor et al., 2003). Far more diverse assemblages appeared later in the early Cambrian (Fortunian to 'Stage 2'), including univalved and bivalved shells, tooth-like structures, arthropod-type exoskeletons, spicules, sclerites, tubes, cones, and ossicles (Bengtson, 2004). Many consider that the rise of predation-pressure as a result of the radiation of bilaterians, particularly in the early Cambrian, promoted the first appearance of hard-parts (Bengtson, 1994, 2004; Bengston & Yue, 1992; Knoll, 2003; Wood, 2011; Wood & Zhuravlev 2012).

This review considers first the Ediacaran redox world, then the affinity, biomineralisation mechanisms, and reproductive habits of Ediacaran skeletal metazoans. Finally, the palaeoecology of Ediacaran metazoan reefs is outlined based on examples from the Nama Group, Namibia, in particular those documented from Driedoornvlagte reef complex (Fig. 1). An accurate understanding of ecosystem functioning during the Ediacaran is vital, as even though its precise role is debated (e.g. Butterfield, 2009; Erwin et al., 2011) ecology is acknowledged to be one of the major drivers of the Ediacaran to Cambrian transition.

The importance of oxygen and the Ediacaran redox world

Animals require oxygen, and therefore the first appearance of marine metazoans during the Ediacaran (580-543 million years ago) has been taken as an indicator that a rise in oxygen, perhaps incrementally, facilitated the evolution of this complexity (De Marias et al., 1992; Canfield et al., 2007; Fike et al., 2006).

Oxygen requirements vary widely in metazoans, and are determined by size, metabolism, mobility, and the presence or absence of a circulatory system and also a biomineralised skeleton (Vaquer-Sunyer & Duarte, 2008). As a result it has been proposed that metazoans may have been limited to small size (<3 mm), thin, non-skeletal, body plans, by the relatively low levels of oxygen of the Proterozoic, with the explosion of larger and ecologically diverse organisms in the late Ediacaran and Cambrian related, in part, to increasing oxygen levels (e.g. Cloud, 1968; Runnegar, 1982). Experimental work has also shown that the oxygen levels necessary to support small, primitive metazoans such as sponges (Porifera) are far lower (Mills et al., 2014) than those required for large, active, and ecologically-important animals such as carnivorous predators (Sperling et al., 2013). But in contradiction to this, there

may be some obligate inhabitants of very low or even anoxic conditions among the Metazoa, for example the Loricifera who, although microscopic, are predators . This is noteworthy as Loricifera and related cycloneuralian worms (members of the Nemathelminthes = roundworms) have a fossil record almost exclusively from the Cambrian and indeed composed a significant part of early Cambrian global and local diversity (Conway Morris, 1985).

In modern marine environments benthic diversity and biomass decreases with bottom-water oxygen levels, as does individual size and abundance until the skeletal macrobenthos is excluded (e.g. Rhoads & Morse 1971). Oxygen availability is a major factor in structuring benthic communities: pelagic-benthic coupling is reduced as are other measures of ecological complexity such as foodweb complexity and community succession. As oxygen levels decrease, large individuals and long-lived equilibrium species are eliminated, and populations shift towards younger individuals, and smaller and short-lived species that possess opportunistic life histories (Diaz & Rosenberg, 1995). The loss of skeletal biota occurs when oxygen drops below ~ 0.10 present atmospheric levels, a threshold therefore postulated to fuel the Cambrian radiation (Rhoads & Morse, 1971). In addition, fluctuating and unpredictable redox conditions are deleterious to some metazoans, so establishing stable oxygenated conditions (Johnston et al., 2012; Wood et al., 2015), even if pO_2 remained relatively low, may have been just as important as a rise in absolute pO_2. Metazoan reefs in particular, require the development of an in situ benthic community of skeletal individuals that forms topographic elevation on the sea floor. Such an ecology requires the maintenance of stable oxic conditions for sufficiently long for the community to persist to reproductive age.

Some suggest, however, that the Ediacaran oxygen transition was a consequence, not a cause, of metazoan diversification, as the pumping activity of poriferans and cnidarians could have augmented the removal of DOC and smaller phytoplankton from the water column, so substantially enhancing its oxygenation (Butterfield, 2009; Lenton et al., 2014). The evolution of Eumetazoa would have shifted oxygen demand to shelf sea sediments and deeper waters, in turn reducing total phosphorus recycling from sediments so reinforcing through positive feedback the shift to a more oxygenated ocean state (Lenton et al., 2014). These authors argue that this could have facilitated the rise of more mobile and predatory animals.

The timing and persistence of oxygen accumulation in Ediacaran oceans, and its relationship to, and feedback from, the rise of metazoans is still poorly understood (Lyons et al., 2014; Russell et al., 2015). But even if oceans had achieved episodes of widespread oxygenation by the late Ediacaran (Kendall et al., 2015), oxygenation was still heterogeneous both temporally and spatially and many continental basins where metazoans are known remained highly stratified (Lyons et al., 2014; Li et al., 2015). These conditions persisted, at least regionally, into the early Cambrian (Canfield et al., 2008).

Oxygenation appears also to have been temporally highly impersistent, even within the shallow sediments of Nama Group, Namibia, which is one of the most well-known successions for both soft-bodied and skeletal metazoan occurrence (Wood et al., 2015). The evolution of ocean chemistry from ~550 to ~541 Ma across shelf-to-basin transects in the Zaris and Witputs Sub-Basins of the Nama Group, Namibia, shows that both sub-basins reveal highly dynamic redox structures, where shallow, inner ramp settings experienced transient oxygenation (Wood et al., 2015). Anoxic conditions were caused either by episodic upwelling of deeper anoxic waters or higher

rates of productivity. Mid-ramp settings, however, particularly during transgression were persistently oxygenated, and it is in these settings where metazoan reefs are found. This suggests that a mid-ramp position may have enabled physical ventilation mechanisms for shallow water column oxygenation such as waves and currents to operate during flooding and transgressive sea-level rise that promoted metazoan reef growth. Alternatively, the reefs may have been bathed in oxygenated bottom water oxygen and perhaps not tied to atmospheric oxygen. It could have been really local but it does constrain that there had to be some there anyway.

Geological setting of the Nama Group, Namibia

To date, all Ediacaran metazoan reefs have been described from the terminal Ediacaran Nama Group, Namibia (~550 – ~541 Ma). The Nama Group was deposited in a foreland basin on the Kalahari Craton that developed during convergence along the Damara and Gariep compressional belts (Grotzinger and Miller, 2008; Gresse and Germs, 1993; Germs, 1974, 1995). The Nama Group is a series of interbedded shallow marine carbonates and siliciclastics deposited in a storm-dominated ramp setting (Saylor et al., 1998). The carbonate Omkyk Member is at the base of the succession. An ash bed that immediately overlies the Omkyk Member has been dated as 548.8 ± 1 Ma (Grotzinger et al., 1995), revised to 547.32 ± 0.31 Ma by Schmitz (2012).

Metazoan reefs have been described from mid-ramp settings of the Omkyk Member of the Kuibis Subgroup at Driedoornvlagte reef complex (Fig. 1C) and Zebra River, and from the Pinnacle Reefs in the Schwarzrand Group (Figs. 1A and B). All Nama reefs consist of either thrombolitic domes, columns and mounds with well-developed internal clotted textures, or stromatolitic domes, columns and mounds with

poorly to moderately well-developed internal lamination (Grotzinger et al., 2005), as well as more massive microbialite mounds . Thrombolite clots are often overgrown by fibrous marine carbonate, interpreted as originally aragonite. Stromatolites are better developed in higher energy proximal conditions of relatively low accommodation: thrombolites form preferentially in high accommodation and low sediment influx settings (Grotzinger et al., 2005). Many cavities of various shapes and size are present in thrombolites which often show a geopetal sediment infill of dolomitised micrite, and precipitation of an isopachous dolomitic rim cement, followed by occlusion of remaining porosity by blocky calcite spar (Grotzinger et al., 2005; Wood & Curtis, 2015).

The Driedoornvlagte reef complex is up to 500 m thick and 7 - 10 km long (Fig. 1C) , and formed down-dip in a deepening, mid-ramp setting during the Transgressive Systems Tract of the Upper Omkyk (or OS2) Member (Grotzinger et al., 2000; Adams et al, 2004). The reef complex is interpreted to represent an isolated platform with two well-defined margins that flanked the platform interior, which attained compacted syndepositional relief from 25 m to about 100 m (Adams et al., 2004).

All metazoan reefs are found in the platform margin of the final (third) accommodation cycle of reef growth (Unit 3M) which grew under increasing accommodation (Adams et al., 2004). The platform margin grew in shallow waters subject to waves and currents, and kept up with rising sea level where complex pinnacle reefs formed. Reefs consist of fused and coalesced thrombolite mounds which increase in size up-section, and were associated with bioclastic grainstones in the lower parts and collapse breccias towards the top as mound relief grew and water depth increased (Adams et al., 2004)**.** Unit 3M mostly aggraded, resulting in a platform relief of up to 50–100 m, and is enclosed by outer-ramp and basinal shale of

the Urikos Member, interpreted to indicate the final stage of the carbonate platform before drowning **(**Grotzinger et al., 2000).

At Zebra River, a series of thrombolite-stromatolite reefs with associated metazoans nucleate and form laterally continuous biostrome layers updip in the TST of the Upper Omkyk Member (Grotzinger et al., 2005). Towards the top of the Upper Omkyk Member the section shallows into grainstone-dominated facies with subordinate shale horizons, containing thinner, discontinuous, microbial biostromes. Rip-up clasts and hummocky cross-bedding indicate storm-dominated conditions throughout.

The Pinnacle Reefs at Swartkloofberg Farm initiate on the flodding surface top of the Huns Member (characterised by interfingering carbonate rocks, siltstones and shales) and form bioherms with a synoptic relief of up to 40 m. After termination of reef growth, the reefs were enveloped by shales of the Feldschuhhorn Member and Spitskopf Member (Fig. 1B).

Here I outline the affinity, mineralogy, and reproductive habits of those associated with reef-building: *Cloudina, Namacalathus,* and *Namapoikia.*

Dramatis personae

Over ten genera with biomineralized skeletons are known from the terminal Ediacaran (~550-541 Ma) (Zhuravlev et al., 2012). Most have been interpreted to be either protistan *sensu lato* or poriferan-cnidarian grades of organization on the basis of overall morphology and the presence of simple skeletal ultrastructures of microgranular or microfibrous types (Wood, 2011).

Cloudina

Cloudina (Figs. 2 and 3) is a globally-distributed, cylindrical fossil found from ~550-541 Ma. *Cloudina* is built of funnel-like, apically flaring tubes set one within the next forming a distinctive cone-in-cone eccentrically-built skeleton (Germs, 1972; Grant, 1990). 5 species have been formally described to date: *C. riemkeae* Germs 1972; *C. hartmanae* Germs 1972; *C. walde*i Hahn & Pflug 1985 [=*C. lucianoi* (Beurlen & Sommer 1957)]; *C. dunfeei* Signor et al. 1987, and *C. carinata* (Cortijo et al. 2010). *Acuticloudina borrelloi* (Yochelson & Herrera 1974) is probably not a cloudinid. Two species have been described from the Nama Group: *Cloudina hartmannae* and *C. riemkeae,* based mainly on size differences. Here the tube diameter of *C. riemkeae* has been previously noted to range from 0.25-2 mm and up to 10 mm long (Wood & Curtis, 2015), and *C. hartmannae* to range from 2.5 to 6.5 mm (Grant, 1990) or up to 8 mm in tube width and 150 mm in length (Wood, 2011; Penny et al., 2014).

Although the affinities of *Cloudina* are problematic, with some preferring an annelid affinity, evidence for dichotomous, asexual budding, as well as microstructure and a closed-tube organisation (Grant, 1990; Vinn & Zaton, 2012) suggests a broadly cnidarian affinity.

Preserved walls are a few tens of microns thick, and individuals show minimal evidence of compaction although folded walls can occur (Conway Morris et al., 1990). *Cloudina*, however, forms the first skeletal packstones/grainstones known in the geological record where individuals show evidence of brittle fracture. *Cloudina* tubes are considered to have formed principally of organic materials with weak biomineralization, inferred to be high-Mg calcite on the basis of preferential dolomitization or preservation as spar-filled molds with microdolomite (Grant, 1990),

and the presence of a microgranular microstructure with epitaxial, fibrous synsedimentary marine cements (Zhuravlev & Wood, 2008).

The *Cloudina* animal is thought to have occupied only the uppermost cones, and has been interpreted as a sessile and gregarious suspension feeder with an epibenthic mode of life attached either to microbial substrates (Cai et al., 2011; Wood, 2011) or to other individuals of the same species (Penny et al., 2014; Wood & Curtis, 2015). The apical part of the tube (or cone) may have served as an attachment site (Cai et al., 2011, 2014; Penny et al., 2014).

The global distribution of *Cloudina* strongly indicates that larval dispersal was in operation. In addition, common close-packing of *Cloudina* individuals infers growth by a regular larval recruitment and settlement: the presence of evidence for dichotomous budding also supports asexual clonal reproduction

Namacalathus

Namacalathus is found nearly globally from ~548 - ~541 Ma (see details in Wood, 2011; Zhuravlev et al., 2015). *Namacalathus* has a stalked cup- or goblet-shaped form up to 35 mm in width and height, with a stem serving as attachment to a substrate and a cup possessing a rounded central opening on the top and usually six, but rounded lumens on lateral facets (Fig. 4E). *Namacalathus* usually displays an almost regular hexagonal radial symmetry in cross section. The stem and outer cup surface can be covered with short, robust spines (Hofmann & Mountjoy, 2001; Zhuravlev et al., 2015). The wall of both the stem and the cup is continuous (Fig. 4E) and up to 100 μm thick.

Namacalathus has been proposed to represent either a possible cnidarian on the basis of an overall goblet-shaped morphology and hexaradial cross section, a protozoan due to small size and an apparent lack of accretionary growth, a stem-eumetazoan, or as a

lophotrochozoan based on a microlamellar ultrastructure and columnar deflections (Fig. 4D; Zhuravlev et al., 2015). The skeleton of *Namacalathus* is often preferentially dolomitised and has been variously interpreted as either calcite or high-Mg calcite on the basis of an absence of neomorphic calcitic textures or moldic preservation (Zhuravlev & Wood, 2008; Zhuravlev et al., 2015).

The near global distribution and common close-packing of *Namacalathus* individuals on bedding planes infers growth by a regular larval recruitment and settlement (Wood & Curtis, 2015). Some individuals of *Namacalathus* also possess daughter cups communicating with a presumable parental cup via stems with inner cavities that are connected directly to the parental cup inner cavity by a lumen while skeletal walls are shared (Figs. 4E and F) and sometimes thickened between new cups and the older one. 3D model reconstructions using SPIERS software from serial sections confirms the skeletal continuity and budding nature of parent and daughter cups (Fig. 4G; Zhuravlev et al., 2015). Such an asexual clonal reproduction is comparable to internal budding which imparts a consistent bilateral symmetry to the entire clonal aggregation.

Namapoikia

Namapoikia rietoogensis is currently known only from the Driedoornvlagte reef complex of the Nama Group (Wood et al., 2002). *Namapoikia* has a robust basal supportive skeleton with a modular, encrusting habit (Figs. 5B and C). *Namapoikia* begins growth as nodular or domal individuals that either coalesce or extend laterally to form sheet-like growths up to 1 m in diameter (Fig. 5B). The skeleton consists of multiple, incomplete, continuously conjoined tubules ranging from 1.5 to 5 mm in diameter, which in transverse section appear labyrinthine to occasionally polygonal (Fig. 5D). The tubules do not appear to expand with growth but tubules grew by

longitudinal fission. Skeletal elements are 0.5 to 3.5 mm in diameter. Growth annulae occur with a spacing of 0.5 to 2.5 mm. Skeletal filling tissue, such as tabulae or dissepiments, is absent, although some structures resemble incomplete tabulae.

This fossil resembles chaetetid sponges or simple colonial cnidarians (Wood et al., 2002). An original aragonitic skeleton is inferred on the basis of preservation as coarse spar mosaic-filled molds and epitaxial, synsedimentary radiating fans of calcitic, neomorphosed aragonitic cement (Wood et al., 2002; Zhuravlev & Wood, 2008). As in modern modular forms, soft-parts probably occupied only the uppermost, youngest, skeletal parts, forming a relatively thin veneer of tissue.

Ediacaran metazoan reef ecology

Diverse reef types have been described from the Nama Group. Here, Ediacaran metazoan reefs are sub-divided into three associations with different major framework builders: 1) Monospecific aggregations of *Cloudina*, 2) *Cloudina – Namacalathus –* thrombolite assemblages, and 3) Thrombolite-dominated metazoan communities.

***Monospecific aggregations of* Cloudina**

Cloudina has been proposed to be a mat-sticker that gained stabilization by growing upwards episodically, tracking sedimentation with concomitant soft-part migration into progressively younger skeletal parts (Seilacher, 1999). Grotzinger et al. (2003) noted the preference for *Cloudina* to be associated with thrombolite reefs, but Hua et al., (2007) concluded that *Cloudina* grew as epifaunal tubes that were oriented horizontally on a soft substrate.

At Driedoornvlagte, however, *Cloudina hartmannae* reefs grew in highly aggregating clusters (Penny et al., 2014), either as smaller coalescing thickets to

create reef framework cavities (Fig. 2B), as single bioherms up to 7 m in diameter (Fig. 2A), or in sheets upon microbial bioherms (Fig. 2C). Some bioherms show intermittent colonisation by stromatolitic laminae. Synoptic relief was probably less than 1 m.

It is noteworthy that *Cloudina* created reef frameworks in the absence of any internal microbial component. Remaining void space between aggregated *Cloudina* individuals, within individual skeletal elements, and within primary reef framework cavities between coalescing clusters is dominantly filled with large botryoids up to 50 mm in radius that represent early marine aragonite cements now neomorphosed to calcite (Fig. 2H). These cements can fill framework cavities up to 0.15m in diameter (Fig. 2B).

Colonising *Cloudina* probably attached to a hard microbial substrate, initially sub-vertically (Fig. 2D). Most *Cloudina* individuals, however, show horizontal or sub-horizontal, sinuous growth. Some individuals show bifurcation to form two sub-horizontal tubes 60 to 90 degrees apart (Penny et al., 2014). Variable orientation of growth in *Cloudina* may have been a response of passive filter-feeders to orient growth into a nutrient-rich current (Penny et al., 2014).

Cloudina individuals are attached to each other in two ways. Colonising individuals settle on the outer walls of older individuals where the apical part of the tube (or cone) served as an attachment site, where subsequent growth is often perpendicular to the orientation of the host tube (Figs. 3D) and shows an increase in tube diameter for the first mm of extensional growth (Penny et al., 2014; Wood & Curtis, 2015). Attachment appears to have been facilitated by some further precipitation of skeletal material, which is now preserved as neomorphosed calcite (Penny et al., 2014). Similarly, *Cloudina* tubes in close proximity are also commonly

cemented together by patch, or meniscus-like, cement features also now neomorphic calcite (Fig. 2F) interpreted as skeletal material between horizontally-growing tubes that added mechanical rigidity to *Cloudina* aggregations (Penny et al., 2014).

Cloudina – Namacalathus – thrombolite assemblages

Intergrown *Cloudina riemkeae* and *Namacalathus* reefs are up to 20 m in height and width have been described from Driedoornvlagte (Wood & Curtis, 2015). Here, synoptic relief could reach several metres.

C. riemkeae formed extensive series densely-intergrown and aggregating assemblages from 30 to 100 mm high, which repeatedly colonised former generations to form either extensive stacked laminar low relief biostromes (Figs. 3A and B), or small mounds, or isolated columnar reef frameworks. Free-standing mounds were often encrusted by stromatolitic laminae.

C. riemkeae was present as sinuous or straight individuals which were dominantly horizontally or sub-horizontally orientated, but sometimes sub-vertical (Fig. 3A). These assemblages are associated with diffuse thrombolitic clots, where clots either encrusted *C. riemkeae*, or individuals were directly attached to clots (Fig. 3D). Remaining void space between aggregated individuals and within individual skeletal elements is filled with large botryoids up to 10 mm in radius that represent early marine aragonite cements now neomorphosed to calcite.

Each *C. riemkeae* assemblage initiated on an undulating sheet of intergrown microbialite and thrombolite 5-25 mm thick, in which grew isolated *C. riemkeae* individuals. Vertically, thrombolite clots become more diffuse as the density of *C. riemkeae* aggregations increases. Cement botryoids increase in size and abundance towards the top of each assemblage until they dominate.

Like *C. hartmannae, C. riemkeae* individuals show budding, and multiple, radiating attachment sites from either each other or thrombolitic clots (Fig. 3D). Cementation between individuals is by patch, or meniscus-like, skeletal features now preserved neomorphic calcite to form chains or rings of multiple attachments, as noted in *C. hartmannae* reefs (Penny et al., 2014).

Namacalathus individuals are occasionally intergrown with *C. riemkeae* (Figs. 3B), but they more often occur as densely aggregating layers of single individuals that succeed *C. riemkeae* assemblages. *Namacalathus* is often very densely-packed, and shows almost tessellate growth (Figs. 4A-C), and there is possible evidence for attachment of adjacent cups. The cup diameter, averaging 5 mm, is consistent within communities over a decimetre scale (Figs. 4A), but there are patches of larger individuals up to 14 mm in cup diameter.

C. riemeake and *Namacalathus* also grew cryptically. Extensive (up to 0.5 m in length and 10 mm high), undulose, laminar crypts are present in some reefs where the reef framework was constructed predominantly by microbialite and thrombolite . Small, clustered individuals of *C. riemeake* and *Namacalathus* grew downwards (pendent) from the crypt walls and ceilings (Fig. 3C) as well as upwards from the crypt floors where they are draped by later geopetal sediment nfill. They appear to have been attached to microbialite or thrombolite substrates, and intergrew with clotted microbialite. A cryptic habit is also noted within neptunian dykes, where similar *Cloudina, Namacalathus* and microbialite/thrombolite intergrowths grew as clusters from dyke walls (Wood & Curtis, 2015).

Thrombolite-dominated metazoan communities

Large (up to 20 m in diameter and 5 m in height), steep-sided, microbial (thrombolite and stromatolite) reefs mounds with subsidiary metazoans are found in several localities in the Nama Group, including Driedoornvlagte, Zebra River, and the Pinnacle Reefs (Grotzinger et al., 2003; Wood, 2011). Well preserved examples reveal that *Cloudina* and *Namacalathus* are entrapped in various relationships within the thrombolite (Grotzinger et al., 2000; Adams et al., 2004; Wood, 2011).

Cloudina is found attached to thrombolite heads, either in a recumbent and sinuous form attached to the upper surfaces (Fig. 6D) or embedded either vertically or sub-horizontally within thrombolite masses (Figs. 6C and E).

While *Namacalathus* had an aggregating habit in low-energy, muddy settings, *Namacalathus* shows a strong preference for microbial substrates, particularly thrombolites. *Namacalathus* has been described from thrombolitic reefs and shallow, platform carbonates in Namibia (Grotzinger et al., 2000; Wood, 2011), thrombolitic reefs in Canada (Hofmann & Mountjoy, 2001) and Oman (Amthor et al., 2003). Large *Namacalathus* individuals are found encased within thrombolites in the Nama Group (Figs. 6A and B). Within thrombolitic settings, *Namacalathus* is commonly encrusted by extensive syn-sedimentary marine cements, particularly fibrous marine botryoids pseudomorphed from aragonite (Fig. 6B). In the Pinnacle reefs, thrombolitic textures appearing at approximately 5 m height above the base of each reef are associated with aggregations of *Namacalathus* (up to 12 mm diameter) which become more prevalent towards the top of the reef (Wood et al., 2015).

Namapoikia encrusts the walls of vertical syn-sedimentary fissures within thrombolitic reefs at Driedoornvlagte (Wood et al., 2002), which formed perpendicular to bedding, and more rarely on open reef surfaces (Fig. 5A). Pore space

within *Namapokia* is commonly filled with syn-sedimentary fibrous marine botryoids (Fig. 5D).

Discussion

The presence of these extensive metazoan reefs demonstrates not only that skeletal metazoans were more important contributors to reef-building in the Ediacaran, but there were also larger, of more variable types, and with more complex ecologies, than previously thought. To date, three broad styles of Ediacaran metazoan reef ecology have been documented but *Cloudina* and *Namacalathus* occupy diverse ecological settings - free standing, associated with thrombolite and microbialite, and also in cryptic habits within thrombolitic reefs (Grotzinger et al., 2000; Wood, 2011; Penny et al., 2014; Wood & Curtis, 2015). By contrast *Namapoikia* was exclusively fissure-dwelling (Wood et al., 2002).

Adaptations to reef-building

Carbonate settings such as reefs, including those of the Ediacaran, are sites of rapid and widespread syn-sedimentary cement formation. Earliest skeletal biotas reach their largest sizes in energetic reef settings where the physiological cost of calcification is even further minimised by the increased precipitation rates conferred by wave action (Wood, 2011). Most skeletons combine minerals with structural organic matter into composite materials, where the physiological cost of producing the mineral is generally small compared to that of the organic matrix (Bengtson, 1994). The earliest skeletal metazoans appear to have mineralized organic-rich skeletons that have retained some degree of flexibility, except in the case of *Namapoikia* which bears a notably large and robust skeleton. Mineralization of an organic precursor skeleton can be inferred. The fact that the earliest skeletal clades have adopted the

minerals aragonite and high-Mg calcite as dictated by ambient ocean chemistry (Mg:Ca and *p*CO2) also strongly suggests that skeletal mineralogy was also highly influenced by extrinsic physico-chemical factors such as temperate and sea water chemistry (Porter ,2007; Zhuravlev & Wood, 2008; Wood, 2011).

The cost of skeletonization is probably far higher in mobile than immobile organisms. Skeletal transportation costs as a fraction of the overall energy budget are not well known, but, for example, data for the marine gastropod *Nucella lamellosa* suggest that the cost of locomotion roughly triples with a doubling of shell weight (Palmer, 1992). It is therefore not surprising that the first skeletal metazoans were immobile, inferring minimal physiological cost.

Solitary Ediacaran skeletal taxa can occupy both soft- and hard-substrates, as noted in *Namacalathus*, where they may show opportunism, i.e. rapid colonisation with high growth rates and short life-cycles (Wood, 2011; Wood & Curtis, 2015). An aggregating habit in solitary organisms, as noted in *Cloudina* and *Namacalathus*, greatly promotes the successful acquisition of substrate, which is often a limiting resource in shallow marine tropical habitats. Dense populations in modern seas are less susceptible than isolated individuals to overgrowth from competitors, predation, larval invasion and infestation, and can also help to stabilise soft-substrates (Jackson, 1983). Likewise, possession of a modular habit, where soft tissue is often a thin veneer over a largely-abandoned skeleton, imparts soft-tissue flexibility and physiological integration so enabling rapid regeneration of surviving parts after partial mortality due to predation (see summary in Wood, 1999).

In order to adapt to high-energy habitats such as reefs, tube-dwelling organisms often build calcareous tubes and some evolve the ability to cement to a hard substrate (Harris, 1990). Possession of a stalk or holdfast (*Namacalathus*), and the ability to attach (*Cloudina*)

or encrust, with a modular habit and large size (*Namapoikia*), provided competitive superiority on hard substrates as well as reducing susceptibility to predation.

Modularity/clonality also allows for asexual as well as sexual reproduction and the possibly of indeterminate growth enables individuals/colonies to reach very large sizes. Size correlates with many measures of success, including increased fecundity. Clonal growth of branching or broadly tubular individuals can lead to extensive and rapid substrate coverage by stands of genetically identical individuals, so minimising competition (see summary in Wood, 1999). Such behaviour is seen in *Cloudina* and *Namacalathus.*

Modern suspension feeding communities are highly efficient feeders because of their ability to self-organize to form complex structures (Gili & Coma, 1998). Benthic suspension feeders form communities that organize into patches or clusters by means of asexual reproduction or dispersal of larvae over short distances. This could imply that extensive, monospecific aggregations of *Cloudina* and *Namacalathus* represent substrates colonised by a limited number of larval spat falls that synchronously colonised large areas of substrate. There are no intermediate individuals between the size ranges of *C. riemkeae* and *C. hartmannae* which suggests, in the absence of any other indications, that *C. riemkeae* and *C. hartmannae* were distinct species, each growing as separate and distinct monospecific stands. This behaviour implies philopatric larval aggregation (where larval offspring settle close to parents) to colonise favourable available substrates. Cloudinids and *Namacalathus* are widely geographically dispersed, suggesting that larvae were also long-lived and capable of wide dispersal. Indeed, some species of *Cloudina* have been noted to have ecological preferences other than reefs in shallow carbonate settings (Cai et al., 2011, 2014; Warren et al., 2011; Wood, 2011).

The elevation afforded by a mineralised skeleton would also have aided tiering of the benthos. Cohen (2005) argues that a benthic habit and increased body size (both resulting from massive mineralization) would have jointly promoted evolutionary success. Mutually-cemented, skeletal individuals also gain further stability by producing topographic relief to create a reef (Penny et al., 2014), and as such this biologically-controlled substrate is important for the successful fostering of future generations (Wood, 1999). Aggregating individuals of *Cloudina* show mutual cementation and no competitive incompatibility.

The earliest metazoan reef communities were differentiated into distinct open surface and cryptic inhabitants from their first appearance (Wood et al., 2002): in the modern such differentiation is structured by numerous competitive and predatory interactions (Wood, 1999). Crypts are often refugia in modern reef environments. Suspension feeders make efficient use of all energy available under the same hydrodynamic conditions (Lesser et al., 1994), with erect forms requiring higher flow rates compared to modular encrusting forms (Sebens and Johnson, 1991). This may explain the ecological segregation seen in Ediacaran reefs of dense aggregations of solitary *Cloudina* growing in energetic shallow waters, with the preferential growth of modular *Namapokia* in lower energy reef fissures.

The rise of the modern carbon cycle

The rise of Ediacaran metazoan reefs marks the modernisation of the carbon cycle in several ways. First, the appearance of calcareous biominerals in metazoans in the Ediacaran changed carbonate sediment production from solely inorganic and microbially-mediated precipitation to a system under considerable biological control. This shift centred upon reefs and their associated sedimentary hinterland. As such this marks a step-change in the workings of the global carbon cycle.

Second, while the Ediacaran is often characterised as a passive ecosystem, metazoan reefs provide evidence for a greater ecosystem role for more active modes of feeding by the late Ediacaran. Where environmental conditions were conducive, in particular stable oxygenated waters, Ediacaran skeletal benthic metazoans could appear in profusion. Such an abundance of inferred benthic suspension feeders has implications for the exploitation of new resources as the prelude to the Cambrian Explosion. The Ediacaran-Cambrian transition and subsequent radiation is an unfolding of evolutionary innovation in order to acquire new resources (Erwin and Valentine, 2013). Metazoan trophic structures had to be constructed from the bottom up, presumably through the innovation first of filter and suspension-feeding, then deposit-feeding, to small herbivores, and finally to primary, secondary and tertiary carnivores (Butterfield, 2001). All this may have been accompanied by increasing standing biomass of suspension-feeders, as well as an increase in individual size and longevity.

By exploiting the plankton, suspension feeders link the benthic and planktonic systems. Suspension-feeding populations exert a major impact on ecosystems as they reduce the concentration of plankton, increasing the retention time on suspended particles on the seafloor, and sharply reducing primary production in the water column so creating a strong energy flow from the pelagic to the benthic system. Modern suspension feeding communities are responsible for a major share of the biomass and energy transport in marine ecosystems, which in turn create feedbacks that regulate primary production directly and secondary production indirectly (Kimmerer et al., 1994). The role of suspension feeders in energy transfer in the marine carbon cycle is thus far more important than would be expected on the basis of their size and abundance alone.

The rise of benthic suspension-feeding metazoans is likely to have led to more active carbon removal: faster sinking fluxes of organic carbon, and an increase in the removal of DOC and smaller phytoplankton from the water column, and more efficient transport and burial of organic carbon to depth (Lenton et al., 2014). As a result, this coupling causes animals to excrete dissolved inorganic and organic waste back into the water column, so becoming major components in the cycling and feedback of essential elements.

The presence of a faster biological pump would have contributed to the ventilation of shelf seas, so shifting oxygen demand over a greater depth of the water column and to shelf sediments. In turn this would have reduced total phosphorus recycling from sediments, so reinforcing the shift to a more oxygenated ocean state (Lenton et al., 2014). Indeed, some have suggested that the appearance of Eumetazoa triggered co-evolutionary feedbacks facilitating the rise of higher oxygen-demanding mobile and predatory animal forms, without the need for any increase in atmospheric oxygen (Butterfield, 2009; Lenton et al., 2014). The more active carbon removal facilitated by abundant suspension feeders would have created a close-coupling of the planktic and benthic metazoan realms with potential for the much-debated consequences for bottom water oxygenation and nutrient cycling.

Conclusions

The oldest known skeletal metazoans appeared in the terminal Ediacaran (~550 Million years (Ma)), and may represent diverse affinities including possible poriferans, stem- or crown-group cnidarians, and basal stem- or total-group bilaterians. All are sessile benthos, found in shallow to mid-ramp marine carbonate settings often associated with various microbial substrates and reefs. The physiological cost of skeletonisation may have been

minimised in such environments by both the high supersaturation of calcium carbonate and the low metabolic demand of an immobile habit. Despite potentially diverse affinities, this skeletal biota shares significant morphological and palaeoecological characteristics: all show evidence for both larval dispersal as well as clonal reproductive strategies, varied adaptations for permanent substrate attachment and mutual cementation, and an aggregating behaviour or encrusting, modular habit. These characteristics are consistent with the growth, reproductive, competitive substrate and anti-predation strategies associated with reef-building.

Ediacaran metazoan reefs can be locally substantial and the skeletal metazoans *Cloudina riemkeae, C. hartmannae, Namacalathus* and *Namapoikia* produced variable reef types with complex ecologies in association with varied microbialite support or influence. To date, Ediacaran metazoan reefs have only been documented from the Nama Group, Namibia: Driedoornvlagte reef complex offers the best documented examples, dated at ~548 Ma. Here, metazoan reefs grew in three associations with differing dominant frameworks: 1) Monospecific aggregations of *Cloudina*, 2) *Cloudina – Namacalathus* – thrombolite assemblages, and 3) Thrombolite-dominated metazoan communities. *C. hartmannae* formed monospecific reefs up to 7 m wide and 3 m high with no microbialite component. *C. riemkeae* formed densely-aggregating assemblages associated with microbialite and thrombolite, each from 30 to 100 mm high, which successively colonised former generations to create stacked laminar or columnar reef frameworks. Isolated *Namacalathus* either intergrew with *C. riemkeae*, or formed dense, monospecific aggregations succeeding *C. riemkeae* frameworks, providing a potential example of environmentally-mediated ecological succession. Thrombolite-dominated metazoan reefs could reach up to 20 m in height and width. *Cloudina* and *Namacalathus* grew closely associated with these framework thrombolites, and *Namapoiki*a, which was

encrusting and modular, reached up to 1m in size occupied almost exclusively neptunian dykes and fissures within large thrombolitc mounds. *Cloudina* and *Namacalathus* also grow cryptically, either as pendent aggregations from laminar crypt ceilings in microbial framework reefs, or as clusters associated with thrombolite attached to neptunian dyke walls.

Such an abundance of inferred suspension feeders by the terminal Ediacaran indicates the exploitation of new resources as the prelude to the Cambrian Explosion, and to the modernisation of the global Carbon Cycle.

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Figure captions

Figure 1: Locations and stratigraphic setting of the Nama Group, Namibia. **A)** Simplified map showing geological setting, subgroups, and sub-basins of the late Ediacaran to early Cambrian Nama Group of southern Namibia (modified from Grotzinger and Miller, 2008) with the locations of 1: Driedoornvlagte, 2: Zebra River, and 3: Pinnacle Reefs. **B)** Stratigraphy of the northern Nama Group (Zaris Sub-basin) illustrating the position of major sequences, ranges of the reef-associated Ediacaran fossils, *Cloudina*, *Namacalathus* and *Namapikia*, and the position of reefs. Arrow indicates the stratigraphic position and age of the dated volcanic ash bed of 547.32 ± 0.31 Ma by Schmitz (2012). **C)** Landsat TM image showing outcrop expression of Driedoornvlagte reef complex. Outcrop dips 40 degrees to the south. Reef is underlain by shelf facies of Omkyk Sequence 1 (OS1), and consists of a lower unit dominated by stromatolitic reefs (SR), overlain by a capping unit of mostly thrombolitic reef (TR). Stratigraphically younger shales of the Urikos Member (Kuibis Subgroup) form the poorly-exposed plain south of the reef (modified from Wood et al., 2002).

Figure 2: Monospecific reefs formed by *Cloudina hartmannae,* from the Omkyk Member, Nama Group, at Driedoornvlagte pinnacle reef complex, Namibia. **A)** Large bioherm, Hammer = approximately 30 mm long; **B)** Small reef with cavity (C) filled with early cement botryoids, Scale bar = 100 mm; **C)** Two generations of laminar thickets, Scale bar = 50 mm; **D)** Initiation of *Cloudina* to microbial substrate attachment (arrowed), Scale bar = 20 mm; **E)** Intergrown *Cloudina*, with pore space filled with early cement botryoids, Scale bar = 50 mm; **F)** Transverse section across a number of *Cloudina* individuals showing meniscus-like calcitic skeletal structures joining tubes together laterally (arrowed); **G)** Intergrown *Cloudina*, with selective dolomitisation of walls and with pore space filled with early cement botryoids, Scale bar = 10 mm; **H)** Intergrown *Cloudina*, with pore space filled with early cement botryoids, Scale bar = 10 mm.

Figure 3: *Cloudina – Namacalathus –* thrombolite assemblages from the Omkyk Member, Nama Group, at Driedoornvlagte pinnacle reef complex, Namibia. **A)** Stacked, communities of *Cloudina riemkeae* showing radiating growth, Scale bar = 50 mm; **B)** Single assemblage from columnar growth showing dense intergrowth of *C. riemkeae* with some *Namacalathus* individuals (arrowed). Skeletons are preferentially dolomitised, Scale bar = 50 mm; **C)** Laminar crypts with downward-growing cement botryoids (B) and clustered individuals of *Namacalathus* and *C. riemkeae* attached to crypt ceiling (arrowed). Crypt floor shows intergrowth of *Namacalathus, C. riemkeae* and thrombolite, Scale bar = 10 mm; **D**) *C. riemkeae* with encrusting thrombolite (T) showing bifurcation (white arrow) and attachment (black arrow), Scale bar = 5 mm**.**

Figure 4: *Namacalathus hermanastes* from *Cloudina – Namacalathus –* thrombolite assemblages from the Omkyk Member, Nama Group, at Driedoornvlagte pinnacle

reef complex, Namibia. **A)** Sub-horizontal surface showing densely aggregating and packed *Namacalathus*. Skeletons are preferentially dolomitised, Scale bar = 50 mm**; B), C)** Tangential section though densely aggregating and packed *Namacalathus*. Skeletons are preferentially dolomitised, and there are multiple generations of early marine dolomitic cement. Scale bars = 20 mm**; B)** Left side (arrowed) shows sections through stalks, right side though cups; **D)** Secondary emission SEM images of etched and polished transverse sections of skeletal wall ultrastructure showing columnar microlamellar inflections (arrowed) and foliated layers. Positions of outer and inner walls are indicated, Scale bar = 200 μm; **E), F)** Transverse section showing parent cup (PC) with budded daughter cups (C) with continuous skeletal walls, Scale bar = 5 mm**; G)** 3D model reconstructions from serial sections, Scale bar = 5 mm (from Zhuravlev et al., 2015).

Figure 5: *Namapokia reitoogensis* from the Omkyk Member, Nama Group, Dreidornvlagte, Nama Group, Namibia, outcrop photos. All Scale bars = 50 mm. A) Several cross-cutting neptunian dykes (arrowed) within a thrombolite mound each with encrusting *Namapoikia*; **B**) Encrusting individual attached to neptunian dyke wall; **C**) Hemispherical individual attached to neptunian dyke wall, in turn encrusted by stromatolite; **D**) Thin section of *Namapoikia* showing tubular and labyrinthine skeletal form.

Figure 6: Thrombolite-dominated metazoan communities from the Omkyk Member, Nama Group, at Zebra River, Namibia. Scale bars = 50 mm. **A**) vertical section showing large individuals of *Namacalathus* (arrowed) attached to thrombolite surfaces or growing between thrombolitc columns, Scale bar = 50 mm; **B**) individuals of *Namacalathus* attached to

thrombolite surfaces with isopachous crusts of early aragonitic ascicular cement, Scale bar = 50 mm; **C**) Vertical section showing numerous individuals of *Cloudina* (some arrowed) trapped within thrombolite, Scale bar = 50 mm, **D**) Recumbent, sinuous *Cloudina* individuals (arrowed) attached to upper surfaces of thrombolite heads, Scale bar = 50 mm, **E)** Vertical section through fine-scale, branching thrombolitic framework showing numerous trapped *Cloudina* individuals (some arrowed).

Figure 7: Reconstruction of a late Ediacaran reef. **1**, Thrombolite, **2,** Neptunian dyke, **3**, Stromatolite, **4,** *Cloudina*, **5**, *Namapoikia*, **6,** *Namacalathus*, **7,** Cement botryoids, **8**, trapped *Namacalathus*, **9**, Sediment. From Penny et al., 2014. Copyright: J. Sibbick.